

THE SYSTEMATICS AND EVOLUTION OF THE SUBSAHARAN AFRICA, SEYCHELLES, AND MAURITIUS SCININE SCINID LIZARDS

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ABSTRACT

Skull osteology and external morphology form the basis for a review of the relationships of the scincine scincid lizards of subsaharan Africa, the Seychelles and Mauritius. There appear to be three natural groups in this area. *Proscelotes* and *Sepsina* constitute the most primitive group in subsaharan Africa, while *Scelotes*, *Melanoseps*, *Scolecoseps* and *Typhlacontias* form a second, perhaps more advanced group. The scincines of the Seychelles comprise two taxa worthy of generic rank (*Pamelaescincus* and *Janetaescincus*, new genera) and together with the monotypic Mauritius genus *Gongylomorphus* form a third natural group. Evolutionary and zoogeographic relationships within each of the three groups are discussed in some detail, but only a passing attempt is made to relate them with each other or with the large, but virtually unknown complex of scincines on Madagascar. In general, this complex seems to have more in common with the mainland *Proscelotes* and *Sepsina* and the three genera of the Seychelles and Mauritius than with the mainland *Scelotes* and its relatives. In addition to the systematic, evolutionary, and zoogeographic discussions there is also a key to the genera of scincines inhabiting mainland Africa south of the Sahara.

INTRODUCTION

Evidence has been presented elsewhere (Greer, 1970) demonstrating that at the subfamily level the Scincines are im-

mediately ancestral to the other three subfamilies of skinks. With the exception of the largest genus (*Eumeces*, 46 species) in the subfamily and the monotypic *Neoseps* of Florida, the Scincinae are entirely Old World in distribution and, again with the exception of the widespread *Eumeces*, show a relict distribution in southcentral and eastern Asia (Fig. 1). For example, the only scincine, with the exception of *Eumeces*, in eastern Asia is *Brachymeles* (13 species) in the Philippines. As one moves west through Asia, no other scincines are encountered until one reaches India, where the monotypic *Barkudia* is known from the regions around Chilka Lake and Calcutta. Further south in India there is a single species of *Sepsophis* in the central and southern part of the subcontinent and two genera, *Nessia* (8 species) and *Chalcidoseps* (1 species), on Ceylon.

Moving still further west, it is not until one reaches Southwest Asia and the Mediterranean area that one encounters widely distributed genera with many species: e.g., *Ophiomorus* (9 species); *Scincus* (12 species); and *Chalcides* (14 species). And it is only south of the Sahara Desert in Africa, Madagascar, and the islands of the western Indian Ocean that the scincines become an important part of the skink fauna (76 of the 136 species of non-*Eumeces* scincines occur in this area).

Two of the other three subfamilies are also found in subsaharan Africa. The Acontinae with approximately 15 species and the



Figure 1. Distribution of the Scincinae, exclusive of *Eumeces*.

Feylininae with 4 species are undoubtedly derived from scincines in Africa, which indicates, along with the present number of species and their distribution in subsaharan Africa, Madagascar, and the islands of the western Indian Ocean, that the scincines have been in subsaharan Africa for much, if not most, of their evolutionary history.

The reasons for the relict distribution of the scincines in south and east Asia and their prevalence in Southwest Asia, Africa, and Madagascar are undoubtedly complex, but may be due in part to the evolution and radiation of the Lygosominae in Southeast Asia and the Australian Region. The lygosomines are undoubtedly derived from the

scincines (Greer, 1970), and are morphologically the most advanced skinks. This group is most numerous and diverse in Southeast Asia and the Australian Region, and its expansion from this area of origin may account in part for the relict distribution of the scincines in south and east Asia. In Southwest Asia, Africa, and Madagascar, the area of the Old World furthest from their area of origin, the lygosomines are fairly well represented by species, but they are not morphologically diverse, i.e., there are not many genera. Presumably the lygosomines are only recent arrivals in this area, and have not yet swamped their ancestral scincine relatives. Perhaps if we could return in several million years, the scincines would show a relict distribution in Africa, Madagascar, and the west Indian Ocean islands as they do in southern and eastern Asia today.

Among scincines, relationships have remained most obscure in that area where extinction (due to competition from the lygosomines?) has done less to sharpen the differences between taxa, i.e., subsaharan Africa, Madagascar, and the islands of the western Indian Ocean.¹ The purpose of this paper is to delimit some of the scincine taxa in this area more clearly than has been the case in the past and to discuss their relationships. As much of the data from this study are derived from comparative skull osteology, the Malagasy scincines, most of which are as yet too poorly known in collections to allow a skull to be prepared, will be largely excluded from the formal taxonomic section of the paper, and their relationships with other scincines will be discussed only in a general way. This is unfortunate, as Madagascar, with its possibilities as a refuge for groups facing extinction from new competitors on the mainland, undoubtedly holds many answers to important questions of scincine evolution. It is doubly unfortunate that Madagascar should be the repository

of this information, as it is unlikely to be much more accessible to collectors in the near future than it has been in the past. Madagascar, then, will probably be the "black box" of our analysis of scincine evolution for a long time to come.

The paper is divided into two major parts. In the first part taxonomic groups are defined, discussed, and defended, and in the second part the evolution and zoogeography of these groups are discussed. The reason for this format is simply that the evolution of groups cannot be discussed without knowing what the groups are that are evolutionarily significant. In addition to this, I have provided a key to the scincine genera of subsaharan Africa.

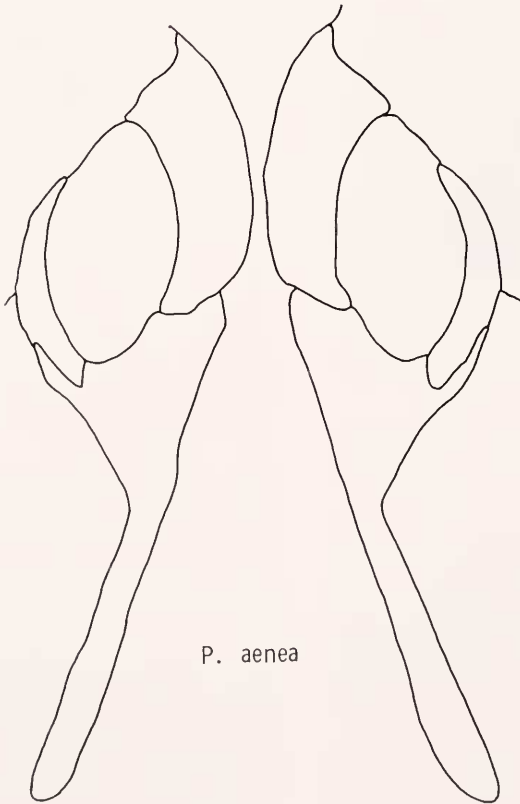
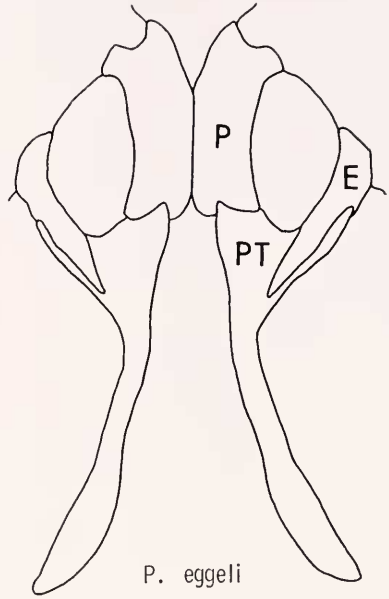
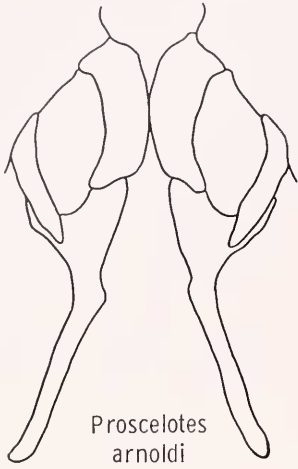
SYSTEMATICS OF THE SUBSAHARAN AFRICA, SEYCHELLES, AND MAURITIUS SCINCINAE

Since the appearance of Boulenger's (1887) third volume of the Catalogue of the Lizards in the British Museum, several authors have discussed the relationships of the scincines of subsaharan Africa, Madagascar, and the islands of the western Indian Ocean (Hewitt, 1921, 1927, and 1929; Barbour and Loveridge, 1928; Smith, 1935; de Witte and Laurent, 1943; Loveridge, 1957). All have relied heavily or exclusively on external characters and one internal character, namely, whether or not the palatine and pterygoid bones meet along the midline of the secondary palate.² Thus each successive discussant has had essentially the same characters available to him that were available to his predecessors. The present study adds new data from the comparison of whole skulls of most of the African, Seychelles, and Mauritius species³ (see Specimens Examined section of paper).

² Unfortunately, the relationships of the palatine and pterygoid bones have often been evaluated without removing the overlying buccal mucosa. This has led to misinterpretations.

³ Species of which whole skulls have been examined are marked with an asterisk (*) in the account of the genera.

¹ The other side of this coin, however, is the preservation of intermediate forms, which makes it easier to understand the evolutionary relationships.



The relevant work of previous authors is discussed under the appropriate taxonomic grouping.

GENERA OF SUBSAHARAN AFRICA

Proscelotes de Witte and Laurent

Proscelotes de Witte and Laurent, 1943, Mém. Mus. Roy. d'Hist. Nat., 2me sér., fasc. 26, p. 13 (Type species, *Scelotes eggeli* Tornier, 1902, by original designation).

Diagnosis. Skull characters: Palatine bones closely apposed or meeting along midline; palatal rami of pterygoids separated and diverging posteriorly; pterygoid teeth absent (Fig. 2). Postorbital bone present and relatively well developed; supratemporal arch strong and fenestra well developed; 17 to 22 maxillary teeth.

External characters: Interparietal small (except in *eggeli*), not touching supraocular scales; a pair of supranasals meeting behind rostral; external ear opening present; 5 fingers and toes (i.e., digital formula, 5-5).

Distribution. Lowlands of Mozambique (*aenea*); from Inyanga south to Melsetter in Rhodesia and Mlanje Mt. in Malawi (*arnoldi*) and Usambara Mts., Tanzania (*eggeli*).

Species. *Aenea** Barbour and Loveridge, 1928; *arnoldi** Hewitt, 1932; *eggeli** Tornier, 1902.

Mode of reproduction. Both *arnoldi* and *eggeli* are known to be live bearing, *arnoldi* producing 5 young (1 female observed—FitzSimons, 1943: 205) and *eggeli*, 3-4 young (3 females observed—Barbour and Loveridge, 1928: 166; and Greer, personal observation). There is no information available on reproduction in *aenea*.

Discussion. With the exception of *eggeli* and *ulugurnensis*, de Witte and Laurent (1943) divided all the subsaharan mainland African scincines, and the genera of what

are now considered two other subfamilies, into two "phyla." One "phylum" was characterized by an interparietal narrower than the frontal and included the genera (as they conceived them) *Sepsina*, *Dumetilia*, *Acontias*, *Acontophiops*, and *Typhlosaurus*. The last three of these five genera are, however, now placed in the subfamily Acontinae (Greer, 1970), and need not concern us here.

The other "phylum" of de Witte and Laurent was characterized by the interparietal's being wider than the frontal. This group included the genera *Herpetosaura*, *Scelotes*, *Scolecoseps*, *Fitzsimonsia*, *Typhlocantias*, *Feylinia*, and *Chabanaudia*. The last two genera are now considered members of the subfamily Feyliminae (Greer, 1970).

Two mainland African scincines, *eggeli* and *ulugurnensis*, however, have frontals that are constricted anteriorly by the supraoculars as in certain Madagascar scincines but not as in any other mainland subsaharan African scincines. This character, along with the fact that the two species are primitive in retaining 5 fingers and toes and seem to have interparietals intermediate in size between the sizes of the interparietal of the two "phyla," suggested to these authors that *eggeli* and *ulugurnensis* formed a relict group ancestral to the two mainland "phyla." The status of these two species was emphasized by their being placed in a new genus of their own—*Proscelotes*.

The interparietal scale is indeed an important taxonomic character in the Scincinae. Unfortunately, however, de Witte and Laurent chose a poor description of the character in the relative size of the scale. A characteristic of the interparietal that is more important, and is reflected less clearly in the size of the scale, is the position of the interparietal relative to the supraoculars;

←

Figure 2. Ventral view of the secondary palate in the three species of the genus *Proscelotes*. Upper left: *P. arnoldi* MCZ 55145; upper right: *P. eggeli* MCZ 24217; bottom: *P. aenea* MCZ 18709. Abbreviations for this and other figures: p, palatine; e, ectopterygoid; pt, pterygoid. Not drawn to scale.

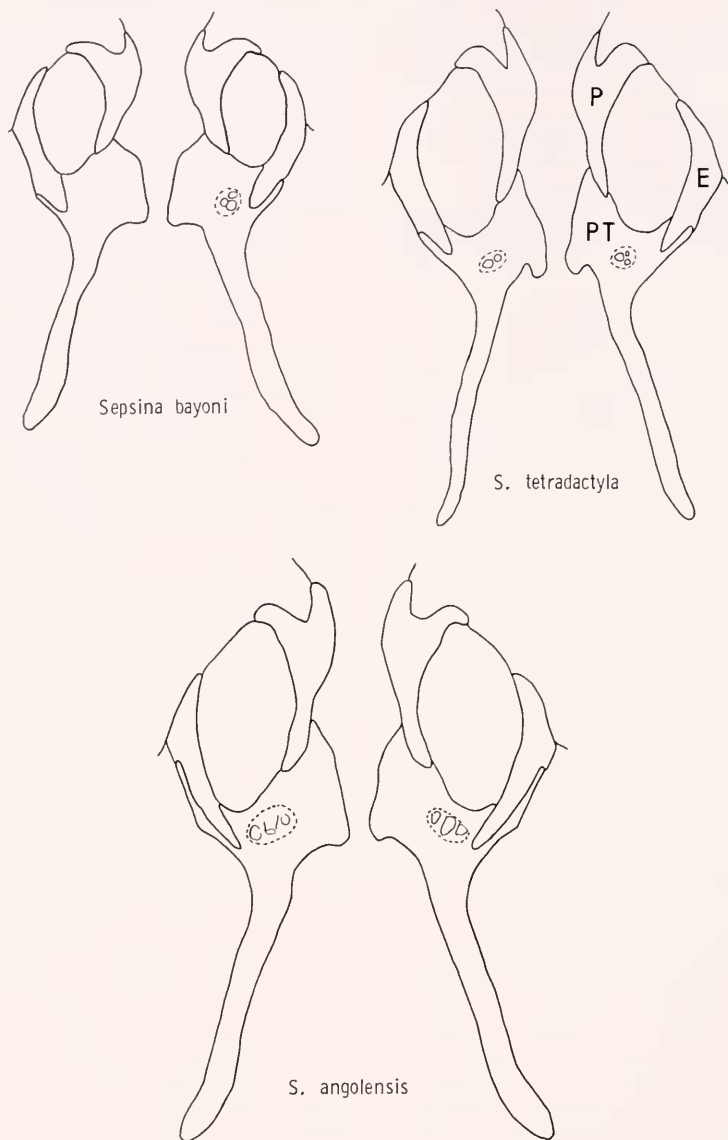


Figure 3. Ventral view of the secondary palate in three species of *Sepsina*. Upper left: *S. bayoni* BM 1967.80; upper right: *S. tetradactyla* MCZ 42885; bottom: *S. angolensis* FMNH 142793. Abbreviations as in Fig. 2. Drawn to scale.

that is, whether the interparietal is in contact with the supraoculars (wider than the frontal) or not in contact with the supraoculars (narrower than the frontal). This character state does not cut across groupings based on skull characters (see diagnoses) and serves to divide the scineines

of subsaharan Africa along essentially the same lines as those proposed by de Witte and Laurent (1943).

With this interpretation of the interparietal, de Witte and Laurent's two species of *Proscelotes* can be easily assigned to one of the two "phyla," and on skull characters

can be shown to be members of species groups within these "phyla." Thus *eggeli*, with a large interparietal, but one not touching the supraoculars, belongs to one "phylum," whereas *uluguruensis*, with the interparietal touching the supraoculars, belongs to the other "phylum."

Within the "phylum" characterized by the interparietal's not touching the supraoculars, *eggeli* is, on the basis of its skull morphology, similar to two other species (*aenea* and *arnoldi*) and forms with these a natural group. The diagnostic characters of this taxon warrant generic recognition. The available name is *Proscelotes*, of which *eggeli* is the type species.

In showing a distinct postorbital bone, i.e., unfused to the postfrontal, and a well-developed supratemporal arch, *Proscelotes* does seem to be rather primitive, as suggested by de Witte and Laurent (1943). The retention of 5 fingers and toes in the three species also supports this supposition.

Sepsina Bocage

Sepsina Bocage, 1866, J. Acad. Sci. Lisboa, vol. 1, p. 62 (Type species, *Sepsina angolensis* Bocage, 1866, by monotypy).

Dumerilia Bocage, 1866, J. Acad. Sci. Lisboa, vol. 1, p. 63 (Type species, *Dumerilia bayonii* Bocage, 1866, by monotypy).

Sepsina (*Rhinoscincus*) W. Peters, 1874, Monatsber. Ak. Wiss. Berlin, p. 373 (Type species, *Sepsina* (*Rhinoscincus*) *tetradactyla* W. Peters, 1874, by monotypy).

Scincodipus W. Peters, 1875, Monatsber. Ak. Wiss. Berlin, p. 551 (Type species, *Scincodipus conigicus* W. Peters, 1875 = *Sepsina bayonii* Bocage, 1866, by monotypy).

Diagnosis. *Skull characters:* Palatine bones widely separated along the midline; palatal rami of pterygoids expanded medially with a tendency toward emargination posteriorly; pterygoid teeth present (Fig. 3). Postorbital bone present and relatively well developed; supratemporal arch strong and fenestra well developed; 12 to 18 maxillary teeth.

External characters: Interparietal small, not touching supraocular scales; a pair of

supranasals meeting behind rostral; external ear opening present; digits 4-4 or fewer.

Distribution. Northern Southwest Africa northward through Angola (*angolensis*) and Cabinda (*bayoni* only) into the southeast part of the Democratic Republic of the Congo (*angolensis*) through the southeastern and eastern sections of the Democratic Republic of the Congo to eastern Tanzania and Malawi (*tetradactyla*).

From comparison of the distribution of *Sepsina* with the distribution of the main vegetation types of Africa (Moreau, 1966: 17, fig. 3), it is clear that *Sepsina* is confined primarily to woodlands (moist and dry), savanna, and steppe, but is excluded from the lowland evergreen forest of west equatorial Africa.

Species. *Angolensis** Bocage, 1866; *bayoni** Bocage, 1866; *tetradactyla** Peters, 1874.

Incertae sedis. *Alberti* Hewitt, 1929; *copei* Bocage, 1873.

On external characters *Proscelotes* can be distinguished from *Sepsina* only on the basis of 5 fingers and toes in the former and no more than 4 fingers and toes in the latter. Digital formulas, however, are so notoriously variable in scincid genera that I hesitate to use such a character in assigning species like *alberti* and *copei*, for which no skull has been available, to genera that are diagnosed primarily on skull characters. For the moment, however, the digital formula is our only clue to the relationships of *alberti* and *copei*, and with only 4 fingers and toes, these two species are considered as most likely belonging in *Sepsina*.

Mode of reproduction. Nothing is known about the mode of reproduction in *Sepsina*.

Discussion. De Witte and Laurent (1943) resurrected the generic name *Dumerilia* Bocage, 1866 for *bayoni* on the grounds that the frontal in this species is wider than it is long, unlike the other species of scincines of the "phylum" consisting of those species with the interparietal narrower than the frontal (essentially the genera *Proscelotes* and *Sepsina* as construed here).

TABLE 1. INTERSPECIFIC VARIATION IN SEVERAL CHARACTERS OF THE GENUS *SCELOTES*.

SEE TEXT FOR DISCUSSION.

Species	Digital formula	Ear opening: present (+) or absent (—)	<i>Herpetosaura</i> (H) or <i>Scelotes</i> (S), fide de Witte and Laurent	Palatines meet (+) or not (—)	Postorbital present (+) or absent (—)	Supratemporal fenestra
<i>capensis</i>	5-5	+ minute	H			
<i>mira</i>	5-5	+ small	H	—	+ small	+ minute
<i>uhugruensis</i>	5-5	+ minute	H ¹	+	—	+ small
<i>caffer</i>	3-3	—	H	+	+ minute	—
<i>limpopoensis</i>	3-3	+ small	H	—	+ small	+ small
<i>bidigittata</i>	0-2	+ minute	H	—	—	+ minute
<i>bipes</i>	0-2	+ minute	S		—	+ minute
<i>kasucri</i>	0-2	+ small	S			
<i>brevipes</i>	0-1	+ minute	H	+	+ small	+ minute
<i>gronovi</i>	0-1	+ minute	S	+	+ thin	—
<i>gautheri</i>	0-1	—	H			
<i>anguina</i>	0-0	—	H	—	+ minute	—
<i>arenicolor</i>	0-0	—	S	—	—	+ minute
<i>bicolor</i>	0-0	—	S			
<i>inornatus</i>	0-0	+ minute	H			

¹ Placed in *Proscelotes* by de Witte and Laurent (1943), but on the criterion of "frontal longer than wide" for distinguishing *Herpetosaura* from *Scelotes* the species is similar to the former genus.

This action seems undesirable since the broad frontal of *bayoni* is probably an adaptation to burrowing habits, which, on the basis of other features of the external anatomy (snout more wedge-shaped and digits reduced to the greatest extent: no forelimbs and a single styliiform hindlimb¹), seem to be more well developed in *bayoni* than in the other species of scincines with the small interparietal south of the Sahara. In the genus *Scelotes* there is a similar trend toward the development of a relatively wider frontal in those species that, on the basis of other morphological characters, seem to be more highly adapted to a burrowing life (see page 10 and Table 1).

Although the two taxa of scincines with

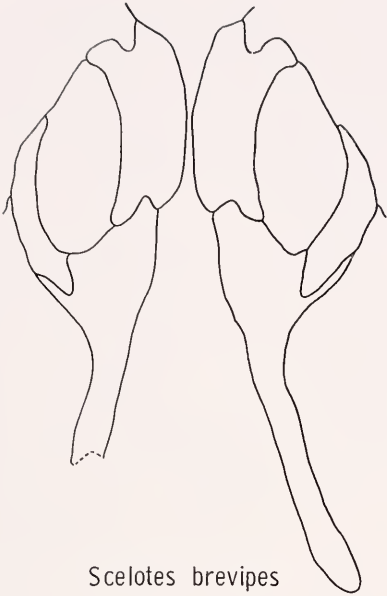
the small interparietal (which fails to touch the frontal) south of the Sahara Desert in mainland Africa, i.e., *Proscelotes* and *Sepsina*, can be recognized on the basis of external characters (*Proscelotes* with 5 fingers and toes and *Sepsina* with 4 fingers and toes or fewer), it should be emphasized that the more important characters distinguishing the two genera are in the skull.

The discrete, well-developed postorbital bone and the pterygoid teeth of *Sepsina* are definitely primitive characters. *Sepsina*, in fact, is the only mainland genus of scincines south of the Sahara to retain pterygoid teeth.

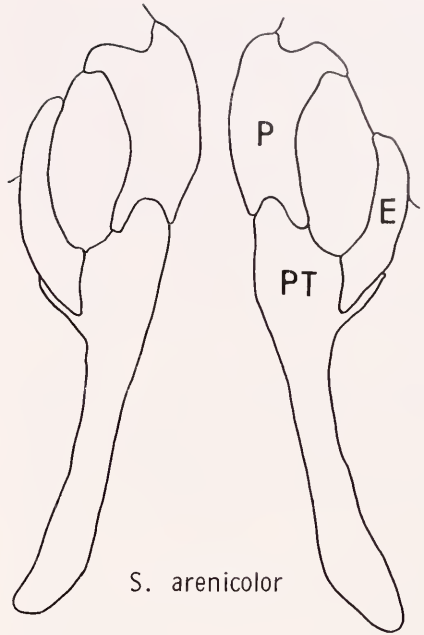
Scelotes Fitzinger

Scelotes Fitzinger, 1826, Neue Class. Rept., pp. 23, 53 (Type species, *Bipes anguineus* Merrem, 1820 = *Scelotes bipes* Linnaeus, 1766, by monotypy). *Zyguis* (not Oken, 1816 or Fitzinger, 1826) Wagler, 1830, Nat. Syst. Amphib., p. 160 (Type species, *Anguis bipes* Linnaeus, 1766, by monotypy). ? *Herinia* Gray, 1838, Ann. Mag. Nat. Hist., vol. 2, p. 332 (Type species, *H. capeusis* Gray, 1838 = ?, by monotypy).

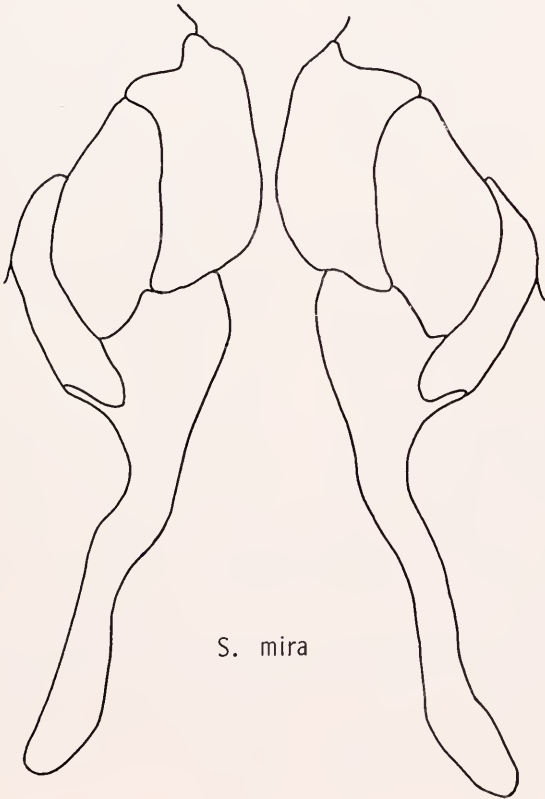
Figure 4. Ventral view of the secondary palate in three species of *Scelotes*. Upper left: *S. brevipes* MCZ 21237; upper right: *S. arenicolor* MCZ 14205; bottom: *S. mira* MCZ untagged specimen. Abbreviations as in Fig. 2. Drawn to scale.



Scelotes brevipes



S. arenicolor



S. mira

Lithophilus (not Fröhlich, 1799) A. Smith, 1849, Illus. Zool. S. Africa, Rept., App., p. 12 (Type species *Lithophilus inornatus* A. Smith, 1849, by subsequent designation of de Witte and Laurent, 1943).

Herpetosaura W. Peters, 1854, Monatsber. Ak. Wiss. Berlin, p. 619 (Type species, *Herpetosaura arenicolor* Peters, 1854, by monotypy).

Scpomorphus W. Peters, 1861, Monatsber. Ak. Wiss. Berlin, p. 422 (Type species, *Scpomorphus caffer* Peters, 1861, by monotypy).

Herpetoseps Boulenger, 1887, Cat. Lizards Brit. Mus., vol. 3, p. 416 (Type species, *Herpetoseps anguinus* Boulenger, 1887, by monotypy).

Diagnosis. Skull characters: Palatine bones meeting or closely apposed on midline; palatal rami of pterygoids separated medially and diverging posteriorly; pterygoid teeth absent (Fig. 4). Postorbital bone present, but small to minute, or absent; supratemporal arch weak, fenestra obliterated by apposition of bones of arch with parietal bone; 11 to 23 maxillary teeth, but only *uluguruensis* with 22 to 23 maxillary teeth, all other species with 11 to 19 teeth.

External characters: Interparietal large, touching supraocular scales; external ear opening present or absent; a pair of supranasals meeting behind rostral (fused only in some *bipes*); digital formula 5-5 to 0-0 (see Table 1).

Distribution. Africa south of an area from southern South-west Africa (*capensis*), east through extreme southern Rhodesia (*limpopoensis* from Beitbridge), and southern Mozambique. Most of the species are found in southern and eastern Africa.

Species. *Anguina** Boulenger, 1887; *arenicolor** W. Peters, 1854; *bidigittata** FitzSimons, 1930; *bicolor* A. Smith, 1849; *bipes** Linnaeus, 1766; *brevipes** Hewitt, 1925; *caffer** W. Peters, 1861; *capensis* A. Smith, 1849; *gronovi** Daudin, 1802; *guentheri* Boulenger, 1887; *inornata* A. Smith, 1849; *kasneri* FitzSimons, 1839; *limpopoensis** FitzSimons, 1930; *mira** Roux, 1907; *uluguruensis** Barbour and Loveridge, 1928.

Mode of reproduction. The mode of reproduction is known for six of the fifteen species of *Scelotes* and all are live bearing

(available clutch sizes follow the species name): *arenicolor*—4 (FitzSimons, 1943: 197); *bidigittatus*—1 to 2 (Pienaar and FitzSimons, 1966: 57); *bipes*—2 (FitzSimons, 1943: 191); *brevipes*—2 (FitzSimons, 1943: 195); *mira*—4 (FitzSimons, 1943: 183); *uluguruensis*—? (Barbour and Loveridge, 1928: 167).

Discussion. Two characters that show a good deal of interspecific variation in *Scelotes* (as conceived here) have been emphasized in generic diagnoses. One of these characters, the complete absence of hindlimbs (used to distinguish the genera *Lithophilus*, *Herpetosaura*, and *Herpetoseps*), is most probably correlated with an increasing tendency toward a burrowing way of life, although actual ecological observations are lacking to support this. The reduction of limbs is also correlated with a reduction in the size of the external ear opening, presumably also an adaptation to burrowing habits (Table 1).

Whether or not the palatine bones touch along the midline of the palate has also been used as a generic character in this group, but it has long been known that this feature is an interspecifically variable character in *Scelotes* (Hewitt, 1921 and 1927; Barbour and Loveridge, 1928; Table 1, this paper).

De Witte and Laurent (1943) revived the name *Herpetosaura* for those species of *Scelotes* with the frontal longer than wide, leaving *Scelotes* to include those species with the frontal wider than long. In Table 1 the generic allocation of the species considered here to be *Scelotes* is given according to de Witte and Laurent. It can be seen from the Table that a frontal wider than long (the "Scelotes" condition) is, in general, correlated with other morphological features indicative of a burrowing way of life. In my opinion this use of characters that show evolutionary trends within a taxon to subdivide that taxon into formal taxonomic groupings, unnecessarily obscures the evolutionary significance of those characters for the sake of taxonomic convenience.

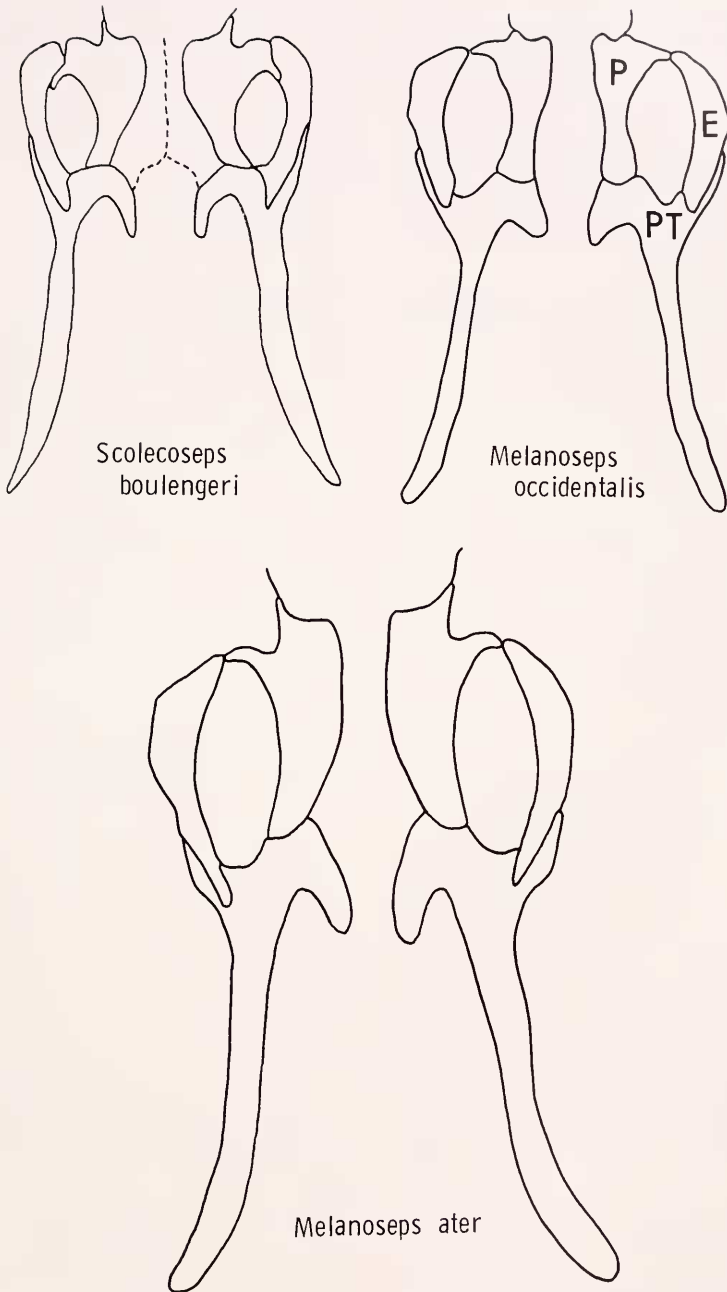


Figure 5. Ventral view of the secondary palate in *Scolecoseps* and *Melanoseps*. Upper left: *Scolecoseps boulengeri* MCZ 18357; upper right: *Melanoseps occidentalis* BM 1907.5.22.6A; bottom: *M. ater rondoensis* MCZ 52487. Drawn to scale. Abbreviations as in Fig. 2.

It should be noted here that *uluguruensis*, a species with a large interparietal touching the supraoculars, was considered a species of *Proscelotes* by de Witte and Laurent (see pages 6–7 above). In the diagnostic skull characters, however, *uluguruensis* is unlike the type species of *Proscelotes* (*eggeli*) and very much like the other species of *Scelotes*.

Melanoseps Boulenger

Melanoseps Boulenger, 1887, Cat. Lizards Brit. Mus., vol. 3, p. 422 (Type species *Herpetosaurus atra* Günther, 1873, by monotypy).

Diagnosis. Skull characters: Palatine bones separated medially; palatal rami of pterygoids expanded medially and emarginated posteriorly; pterygoid teeth absent (Fig. 5). Postorbital bone absent; supra-temporal arch weak and fenestra obliterated by apposition of bones of the arch with the parietal bone; 10 to 13 maxillary teeth.

External characters: Interparietal large, touching supraoculars; a pair of supranasals meeting behind rostral; no external ear opening; limbless.

Distribution. Extreme southern Kenya south through Tanzania and Malawi to the Zambesi (*ater*) and west through the Democratic Republic of the Congo, and extreme northeastern Angola to Cameroon and Fernando Poo (*occidentalis*). In addition, Sternfeld (1911) reports a single specimen of *occidentalis* from Windhuk, Southwest Africa. This locality is, however, some distance from the range indicated by other specimens of *occidentalis* and is also from a considerably drier area than any other specimens. For these reasons the record should perhaps be regarded with suspicion (Mertens, 1955).

Species. *Ater** Günther, 1873 (six subspecies); *occidentalis** W. Peters, 1877.

Mode of reproduction. Personal observations on *M. ater misukuensis* indicate that the species is live bearing. Six gravid females had 2 to 4 (average = 3.0) developing eggs in a clutch.

Discussion. The generic distinction of *Melanoseps* from *Scelotes*, which has been

argued for by most authors (Boulenger, 1887; Tornier, 1901; Loveridge, 1957; Laurent, 1964), is confirmed on the basis of skull morphology: no *Scelotes* has the medially expanded and posteriorly emarginated palatal rami of the pterygoids seen in *Melanoseps* (Figs. 4, 5).

De Witte and Laurent (1943) regarded *Melanoseps* as a synonym of *Scelotes*. However, when Loveridge (1957) pointed out that *Melanoseps* is "associated with primary forest, either montane or gallery," a habitat from which *Scelotes* is largely excluded, Laurent (1964) considered these ecological differences, along with the morphological differences, sufficient evidence for the generic separation of *Melanoseps* from *Scelotes*.

Melanoseps appears to be a derivative of a *Scelotes*-like ancestor that has evolved primarily in the evergreen montane and lowland forests of central Africa.

Scolecoseps Loveridge

Scolecoseps Loveridge, 1920, Proc. Zool. Soc. London, p. 159 (Type species, *Scolecoseps bou-lengeri* Loveridge, 1920, by monotypy).

Diagnosis. Skull characters: Palatines widely separated; palatal rami of pterygoids expanded slightly toward midline and deeply emarginated posteriorly, somewhat as in *Melanoseps*; pterygoid teeth absent (Fig. 5). Postorbital bone absent; supra-temporal arch weak and fenestra obliterated by apposition of bones in arch with parietal bone; twelve maxillary teeth.

External characters: External naris in a large rostral and connected with the posterior edge of the rostral through a horizontal suture somewhat as in *Typhlacoutias* (Scincinae) or the subfamily Acontinae. Interparietal large, touching supraoculars; a pair of supranasals meeting behind rostral; no external ear opening; limbless.

Distribution. Lumbo, Mozambique (*boulengeri*) and Dar es Salaam to Kilwa, Tanzania (*acontia*).

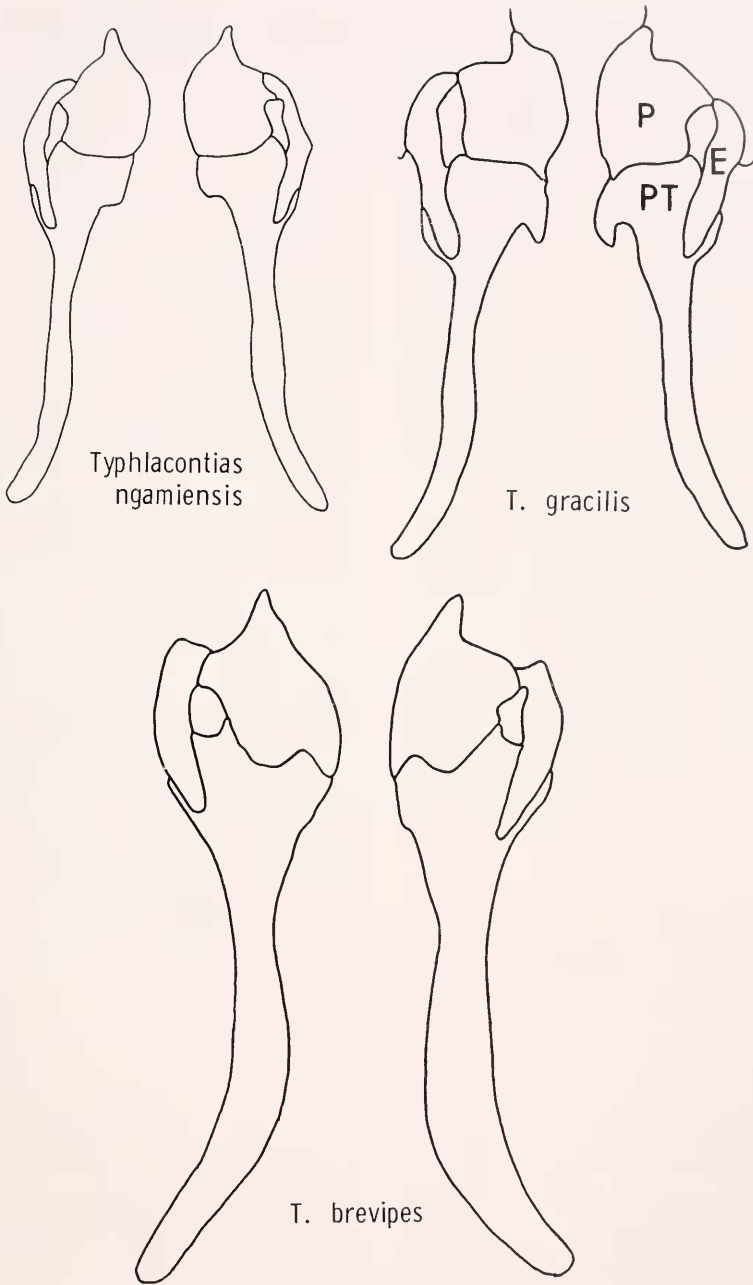


Figure 6. Ventral view of the secondary polote in three species of *Typhlacontias*. Upper left: *T. ngamiensis* FMNH 142787; upper right: *T. gracilis* USNM 159338; bottom: *T. brevipes* MCZ 96702. Abbreviations as in Fig. 2. Drawn to scale.

Species. *Acontias* Werner, 1912; *boulengeri** Loveridge, 1920.

Mode of reproduction. Absolutely nothing is known about the mode of reproduction in the two species of this rare genus.

Discussion. I have been able to examine the secondary palate only in the type species of this genus, *boulengeri*. The palate is similar to that of *Melanoseps*, but the large rostral seems distinct enough to warrant generic separation from *Melanoseps*.

I have not been able to see the palate in *acontias*, the other species in the genus. The enlarged rostral of this species is similar to that of *Scolecoseps boulengeri*, but it is also similar to the rostral of some *Typhlacontias*. Since palatal characters are the only basis we would have for changing the generic status of *acontias*, it seems best to follow current taxonomic opinion (de Witte and Laurent, 1943; Loveridge, 1957) and retain *acontias* in *Scolecoseps*.

These two species of skinks are extremely poorly represented in herpetological collections, and virtually nothing is known of their ecology. The absence of both an external ear opening and limbs would indicate that the genus is burrowing or at least cryptic in habits.

Typhlacontias Bocage

Typhlacontias Bocage, 1873, J. Acad. Sci. Lisboa, vol. 15, p. 5 (Type species, *Typhlacontias punctatissimus* Bocage, 1873, by monotypy).

Fitzsimonsia de Witte and Laurent, 1943, Mém. Mus. Roy. d'Hist. Nat., 2me sér., fasc. 26, p. 33 (Type species *Typhlacontias brevipes* FitzSimons, 1939, by monotypy).

Diagnosis. Skull characters: Palatine bones only slightly longer than wide, separated medially; palatal rami of pterygoids expanded laterally, but not meeting medially, and emarginated posteriorly (*gracilis*) or not (*brevipes* and *ngamiensis*); pterygoid teeth absent (Fig. 6). Postorbital and jugal bones lacking; supratemporal arch weak and fenestra obliterated by the apposition of the bones in the supratemporal arch with the parietal; five to six maxillary teeth.

External characters: Interparietal large, touching supraoculars; three median, transversely enlarged head scales between the rostral and interparietal instead of a pair of supranasals and two median, transversely enlarged head scales; no external ear opening; limbless except for *T. brevipes*, which has a rudimentary hind leg.

Distribution. Collecting records for the genus are few and widely separated but stretch from southern Angola and Southwest Africa east through Botswana to the Upper Zambesi region and extreme southeastern Rhodesia. This area is covered by the desert, subdesert, and dry woodlands, steppe vegetation types of Moreau (1966, fig. 3).

Species. *Bogerti* Laurent, 1966; *brevipes** FitzSimons, 1938; *gracilis** Roux, 1907; *ngamiensis** FitzSimons, 1932; *punctatissimus* Bocage, 1873; *rohani* Angel, 1923.

Mode of reproduction. The only information on the mode of reproduction in this genus is the statement by Laurent (1964: 84) in regard to *T. bogerti*, which would indicate that the species is live bearing: "Le grand Paratype contient des *embryons avancés* dont les yeux sont fort développés." The italics are mine.

Discussion. The large interparietal indicates that *Typhlacontias* is a relative of *Scelotes*, and like *Melanoseps* the genus is probably a *Scelotes* derivative. But unlike *Melanoseps*, which has evolved in the moist evergreen lowland and montane forest of central Africa, *Typhlacontias* seems to have evolved in the arid areas of southern Africa. The adaptations of the genus, e.g., absence of an external ear opening, the almost complete reduction (*brevipes*) or absence of the limbs, and the large rostral, seem to be indicative of highly developed burrowing habits, but ecological data by which to judge this supposition are lacking. That the group is not just a composite of independently evolved *Scelotes*, well adapted to a burrowing life, is indicated by the large single postrostral scale, the unique proportion and relationships of the palatal bones,

the absence of a jugal bone, and the low number of maxillary teeth—features not found in those *Scelotes* (*brevipes*, *gronovi*, *guentheri*, *anguina*, *arenicolor*, *bicolor*, and *inornatus*) similarly adapted in other features of their morphology to a burrowing life.

Typhlacontias brevipes has the external naris situated close to the posterior edge of the rostral and bordered posteriorly by a small postnasal scale; this is a *Scelotes*-like feature. It also retains minute posterior limbs unlike other *Typhlacontias*. Because of these features de Witte and Laurent (1943) created a new genus, *Fitzsimonsia*, for the species. Such special taxonomic recognition seems unjustifiable to me as it obscures evolutionary relationships. *Typhlacontias brevipes* is best viewed as the most primitive, i.e., the most *Scelotes*-like, of its genus and relates *Typhlacontias* directly with *Scelotes*. *T. brevipes* possesses the large single postrostral scale and palatal characters of *Typhlacontias* and lacks the jugal bone as do other *Typhlacontias*, but it resembles *Scelotes* in the position of the external naris and the minute hindlimbs.

It is interesting to note that among the scincines of subsaharan Africa only *Scelotes bipes* has postrostral scales (supranasals) that are sometimes fused to form a single median transverse scale. This condition is characteristic of *Typhlacontias* and is further evidence that a *Scelotes* was probably ancestral to *Typhlacontias*.

MAURITIUS AND SEYCHELLES GENERA

With the exception of Bermuda, which harbors the endemic *Eumeces longirostris*, Mauritius and the Seychelles are the most remote oceanic islands on which scincines are known to occur now or in the recent past. On the Seychelles there are three species (*gardinieri*, *braueri*, and *veseyfitzgeraldi*) that have always been called either *Scelotes* or *Amphiglossus*, generally by authors using these two generic names in their widest, catchall sense. The single scincine on Mauritius (*bojeri*) and the

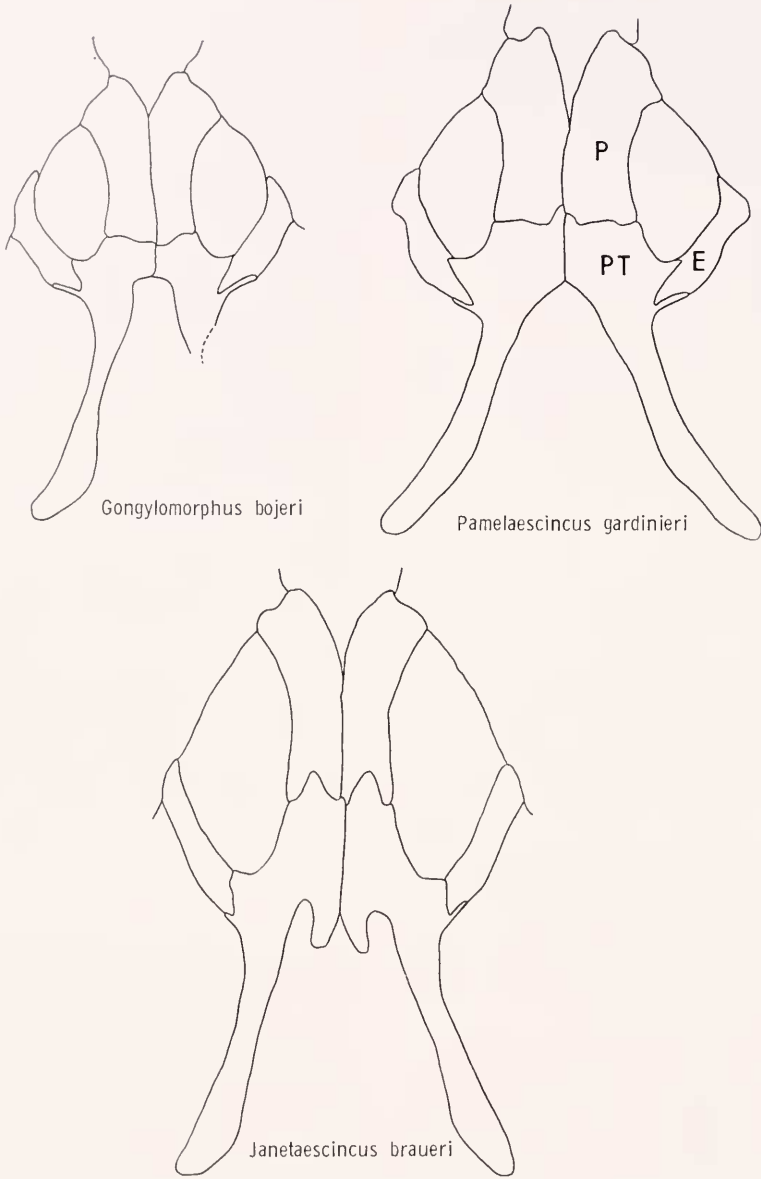
neighboring islands¹ on the bank just north of the main island has generally been placed in the genus *Scelotes* or referred to a monotypic genus, *Thyrus*. Loveridge (1957) has noted that the generic name *Thyrus* for the endemic Mauritius scincine is antedated by the name *Gongylomorphus*.

The scincines of the Seychelles and Mauritius show certain peculiar features in their skull osteology that have not been encountered in any other scincine species for which skulls are available. The most striking of these features is an extensive secondary palate (Fig. 7) formed by the medial apposition of the palatine bones (seen in a less well-developed state among scincines only in *Proscelotes* and some *Scelotes*) and the palatal rami of the pterygoids (unknown in any other scincine to date). In addition, there are 11 teeth on the premaxillae in the Mauritius and Seychelles scincines, whereas all other scincines have only 10 (only a few *Brachymeles*) or fewer (generally fewer than 9 in most other scincines).

Slightly less significant, but of value in recognizing groupings of scincines in Africa, is the presence of a large, distinct post-orbital bone (partially fused to the post-frontal in the single skull of *braueri* examined) and a well-developed supratemporal arch.

These similarities, especially for scincines, would be indicative of close relationship in other species groups. But the fact that these species occur on two widely separated oceanic island banks poses a serious zoogeographic problem and raises the possibility of convergence as an alternative explanation for the unique similarities among the four species. There is, however, no other evidence suggesting that the similarities among these species are convergent. Indeed, the independent evolution of a remarkably advanced secondary palate (for scincines) in these lizards seems less cred-

¹ This species is actually known only from subfossil material on Mauritius itself (Hoffstetter, 1945 and 1949), although it still occurs on several small islands just north of Mauritius (Vinson, 1965).



Gongylomorphus bojeri

Pamelaescincus gardinieri

Janetaescincus braueri

Figure 7. Ventral view of the secondary palate in *Gangylamorphus*, *Pamelaescincus* and *Janetaescincus*. Upper left: *Gangylamorphus bojeri* MCZ 46677; upper right: *Pamelaescincus gardinieri* BM 1910.3.18.91; bottom: *Janetaescincus braueri* BM 1910.3.18.33. Abbreviations as in Fig. 2. Not drawn to scale.

ible to me than the notion of their close relationship in spite of the zoogeographic problem raised by that relationship. For the present, therefore, I am regarding the scincines of Mauritius and the Seychelles

as a closely related group with a remarkable distribution.

In spite of the remarkable similarities which serve to distinguish them as a group apart from all other scincines, the Seychelles

and Mauritius scincines (4 species) themselves show certain peculiar morphological features that warrant their separation into 3 genera as follows:

Gongylomorphus Fitzinger

Gongylomorphus Fitzinger, 1843, Syst. Rept., p. 22 (Type species, *Gongylus bojerii* Duméril and Bibron, 1839 = *Scincus bojerii* Desjardin, 1831, by monotypy).

Thyrus Gray, 1845, Cat. Specimens Lizards Coll. British Mus., p. 124 (Type species, *Scincus bojerii* Desjardin, 1831, by monotypy).

Diagnosis. *Skull characters:* Palatine bones and palatal rami of pterygoids meeting medially; palatal rami of pterygoids "squared-off," not emarginated posteriorly as in the following two genera; pterygoid teeth absent (Fig. 7). Postorbital bone distinct, well developed; supratemporal arch well developed; 16 teeth on maxilla and 11 teeth on premaxillae.

External characters: Interparietal small, not touching supraoculars; frontoparietals present (absent in all other subsaharan Africa, Madagascar, or west Indian Ocean island scincines); ear opening a horizontal slit; 38 longitudinal scale rows at midbody; digits 5-5.

Distribution. At present *G. bojeri* occurs only on several small islands (Round, Plate, Coin de Mire, and Forquets) lying on the shallow bank just north of Mauritius. The species is, however, known from subfossil remains on Mauritius (Mare aux Songes), and Vinson (1965) conjectures that in the past *G. bojeri* also occurred on Reunion.

Species. *Bojeri** Desjardin, 1831.

Discussion. One of the most intriguing questions centering around *bojeri* is its recent extinction on the main island of Mauritius while it persists on the small bank islands just north of the main island. Interestingly enough, however, *bojeri* is not unique in being subfossil on Mauritius while persisting on a bank island. *Casarea*, a monotypic genus of boiid snakes, is also subfossil on Mauritius in the same locality as *bojeri* (Mare aux Songes), but persists on Round Island in the bank islands (Hoff-

stetter, 1960). Similarly the giant skink *Didosaurus mauritiannus* is subfossil on Mauritius (Mare aux Songes) while its very close relative (Greer, personal observation), *Leioliopisma telfairi*, exists only on Round Island. In addition, there are endemic species on the bank islands (Round Island) which are not known today or in the past on Mauritius, but which have probably either evolved *in situ* or are relict populations of species no longer extant on Mauritius, i.e., the gecko *Phelsuma guentheri* and the monotypic boiid genus *Bolyeria*.

These data strongly suggest that extinction among the endemic reptiles of the Mauritius bank has been greater on the main island than on the bank islands. The reasons for this differential extinction are unknown, but it is perhaps significant that a dramatic differential alteration of the ecology of these islands took place when man and his animals arrived and colonized the main island of Mauritius but, until quite recently, left the small bank islands relatively undisturbed. The case is unproved as yet, but man and his animals have already been deeply implicated in the extinction of the Mauritius birds, and their guilt may be equally great when the case of the reptiles comes to trial.

Pamelaescincus new genus¹

Type species. *Scelotes gardinieri* Boulenger, 1909, Trans. Linn. Soc., ser. 2, Zool., vol. 12, p. 298.

Diagnosis. Similar to *Gongylomorphus* and the following genus and differing from all other scincine skinks in having the palatines and palatal rami of the pterygoids meeting medially to form a broad secondary palate (Fig. 7), and in having 11, instead of 10 or fewer, premaxillary teeth.

Among the Seychelles and Mauritius scincines, which appear to be the genus' closest relatives, *Pamelaescincus* is most similar in palatal characters to *Gongylo-*

¹ The genus is named after Pamela, the older of my two sisters.

morphus, but differs from this monotypic Mauritius genus in lacking both the frontoparietal scales and the clear spectacle in the lower eyelid.

Pamelaescincus is similar to other Seychelles scincines in lacking frontoparietals (which all other subsaharan Africa and Madagascar scincines have) and in having scaly eyelids; but differs from these species in lacking the posterior emargination of the palatal rami of the pterygoids (Fig. 7), in having 5 instead of only 4 fingers, and in having a high midbody scale count (30 to 34 instead of 22 to 24).

Distribution. The single species in the genus is reported from the following islands in the Seychelles archipelago: Mahé, Praslin, Silhouette, and Frigate.

Species. *Gardinieri** Boulenger, 1909.

*Janetaescincus*¹ new genus

Type species. *Scelotes braueri* Boettger, 1896, Zool. Anz., vol. 19, p. 349.

Diagnosis. Similar to *Gongylomorphus* and *Pamelaescincus* and differing from all other scincines in having the palatines and palatal rami of the pterygoids meeting medially to form a broad secondary palate (Fig. 7); and in possessing 11, instead of 10 or fewer, premaxillary teeth.

In skull morphology *Janetaescincus* differs from *Gongylomorphus* and *Pamelaescincus* in having the palatal rami of the pterygoids emarginated posteriorly (Fig. 7). On the basis of external characters the new genus is easily distinguished from *Gongylomorphus* and *Pamelaescincus* by means of its lower midbody scale count (22 to 24 instead of 30 to 35), and by the possession of only 4 fingers instead of 5. *Janetaescincus* also lacks the frontoparietals and clear spectacle in the lower eyelid of *Gongylomorphus*. The circular external ear opening is relatively smaller in *Janetaescincus* than in *Pamelaescincus* and, of course, is easily distinguishable from the horizontal slit in *Gongylomorphus*.

¹ The genus is named after Janet, the younger of my two sisters.

Distribution. The two species of *Janetaescincus* are recorded from the following islands in the Seychelles: Mahé (*braueri*), Frigate (*veseyfitzgeraldi*), and Silhouette (both species).

Species. *Braueri** Boettger, 1896; *veseyfitzgeraldi* Parker, 1947.

SCINCINES OF MADAGASCAR

Too little is known about the skull morphology of Malagasy scincines to make any formal taxonomic decisions on this basis. Enough is known, however, to bring out the broad relationships between the scincines of Madagascar and the scincines of subsaharan Africa and the islands of the west Indian Ocean.

The single external feature that is shared by all Malagasy scincines and that serves to align them with certain other groups of scincines is the small interparietal scale. In the Malagasy species, as in *Proscelotes* and *Sepsina* in Africa, *Gongylomorphus* on Mauritius, and *Pamelaescincus* and *Janetaescincus* on the Seychelles, the interparietal does not touch the supraocular scales, and, of course, as in all scincines south of the Sahara and on the islands of the west Indian Ocean, except for *Gongylomorphus*, there are no frontoparietal scales.

Although the skulls of only a very few species of Malagasy scincines have been examined (see Specimens Examined section of paper), those skulls and *in situ* palates that have been examined show certain broad similarities. For instance, the palatines and palatal rami of the pterygoids do not meet medially in any of the skulls examined, and the palatal rami of the pterygoids are not expanded medially nor are they emarginated posteriorly. In other words, the palate is simple and is most similar to that of *Proscelotes* and *Scelotes*.

Most of the skulls of Malagasy scincines examined also have a separate and well-developed postorbital bone similar to the postorbital bone in *Proscelotes*, *Sepsina*, *Gongylomorphus*, *Pamelaescincus*, and *Janetaescincus*, that is, those genera with a

small interparietal not touching the supra-ocular scales.

In a very general way, therefore, the relationships of the Malagasy scincines seem to be closest to the African *Proscelotes* and *Sepsina* and the west Indian Ocean island genera *Gongylomorphus*, *Pamelaescincus*, and *Janetaescincus*. The strongest evidence at hand for this broad relationship is the small size of the interparietal scale and the well-developed postorbital bone in these skinks. Admittedly this seems to be thin evidence, but it is at present all we have to go on.

EVOLUTION AND ZOOGEOGRAPHY OF THE SUBSAHARAN AFRICA, SEYCHELLES, AND MAURITIUS SCINCINAE

Evolution

It is evident from the discussion above that three major groups of scincines are recognizable in subsaharan Africa, the Seychelles, and on the Mauritius bank. I wish to discuss the evolution of these three groups below.

(1) One of the three groups, the *Proscelotes-Sepsina* group, is the only taxon of subsaharan Africa scincines with a small interparietal which fails to touch the supra-oculars. This is a primitive group in that the postorbital bone remains large and the supratemporal fenestra is open. In addition, *Proscelotes* retains the primitive digital formula of 5-5, and *Sepsina* is the only scincine in subsaharan Africa to retain pterygoid teeth. Both *Proscelotes* and *Sepsina* also seem to be much less closely adapted to a burrowing way of life than are many *Scelotes* and all *Melanoseps*, *Typhlacontias*, and *Scolecoseps*. It is impossible at this point, however, to say that either genus, *Proscelotes* or *Sepsina*, is more primitive than, and possibly ancestral to, the other. *Proscelotes* retains pentadactyl limbs (primitive), but lacks pterygoid teeth (advanced); whereas *Sepsina* has reduced the number of digits to 4-4 or fewer (advanced), but retains pterygoid teeth (primitive).

(2) The genera *Scelotes*, *Melanoseps*, *Scolecoseps*, and *Typhlacontias* seem to form another tightly-knit taxon immediately recognizable on the basis of the large interparietal, which is in contact with the supra-ocular scales. The group seems to have adopted a more secretive, subterranean way of life than have *Proscelotes* and *Sepsina*, and many of the adaptations to this way of life, as well as other less obvious adaptations of *Melanoseps*, *Scolecoseps*, and *Typhlacontias*, can be seen as trends within *Scelotes*. Some of the trends in *Scelotes* which appear to portend the adaptations of the other three genera are discussed below.

Loss of limbs: The species of *Scelotes* show various stages of limb and digit reduction from the primitive five-fingered, five-toed condition to the complete loss of all external traces of limbs (Table 1). All species of the other three genera except for *Typhlacontias brevipes*, which retains a single styliform hindlimb, are entirely limbless.

Loss of external ear opening: Roughly correlated with the loss of the limbs in *Scelotes* is the reduction in size and, ultimately, the loss of the external ear opening (Table 1). *Melanoseps*, *Scolecoseps*, and *Typhlacontias* also lack an external ear opening.

Fusion of supranasals: Although all species of *Scelotes* have paired supranasals which meet directly behind the rostral, some populations of *S. bipes* have these scales fused in a high proportion of the individuals. The fusion of the supranasals results in a single band-like scale behind the rostral, which is reminiscent of the single transversely enlarged "internasal" scale of *Typhlacontias*. *Melanoseps* and *Scolecoseps*, however, have the primitive paired supranasals of *Scelotes*.

Articulation of stapes and quadrate: In all the skulls of *Melanoseps*, *Scolecoseps*, and *Typhlacontias* examined (see Specimens Examined section), the bony shaft of the stapes is short and stout and projects posterolaterally to articulate directly with

a ventrally projecting nub from a posterior extension of the quadrate. The same relationship between the stapes and quadrate is also seen in *Scelotes arenicolor*, while a very close approximation to the *Melanoseps*, *Scolecoseps*, *Typhlacontias* condition (stapes abuts quadrate obliquely) can be seen in *Scelotes caffer* and *S. anguina*. Other species of *Scelotes*, however, have the more usual stapes-quadrate relationship in which the relatively more slender and longer stapes is directed laterally and articulates with the tympanum via cartilage. From the few skulls of *Scelotes* examined, there appears to be little correlation among the relationships of the stapes and quadrate, and the degree of loss of the digits, and the reduction in size of the external ear opening.

Reduction and loss of the postorbital bone: In *Scelotes* there is a tendency to reduce and ultimately lose the postorbital bone (Table 1), and in *Melanoseps*, *Scolecoseps*, and *Typhlacontias* the postorbital is lacking altogether. Even in its most well-developed condition in *Scelotes*, the postorbital bone is generally smaller than in *Proscelotes* and *Sepsina*.

Obliteration of supratemporal fenestra: Whereas the supratemporal arch is strong and the supratemporal fenestra well developed in *Proscelotes* and *Sepsina*, the arch is weak and the fenestra, at best, small in some *Scelotes*. In the remaining *Scelotes* and in *Melanoseps*, *Scolecoseps*, and *Typhlacontias* the fenestra is obliterated entirely by the close apposition of the postfrontal, postorbital (when present), and squamosal bones with the parietal.

Although it is fairly clear that *Melanoseps*, *Scolecoseps*, and *Typhlacontias* are relatives of *Scelotes* and probably share a common ancestry with *Scelotes*, the relationships of the taxa are not entirely clear. *Melanoseps* differs morphologically from *Scelotes* only in showing posterior emarginations of the palatal rami of the pterygoids, and *Scolecoseps*, in turn, differs from *Melanoseps* primarily in having the external naris situated well forward in the large

rostral scale. The sequence *Scelotes* → *Melanoseps* → *Scolecoseps* would be a reasonable morphological sequence by which to explain the evolution of these taxa. *Typhlacontias*, on the other hand, with its one species (*brevipes*) with a styliform hindlimb, may have evolved independently from a *Scelotes*-like ancestor.

(3) Finally, a third group, whose genera have been discussed in a formal systematic manner above, consists of the monotypic Mauritius *Gongylomorphus*, and the two genera (3 species), *Pamelaescincus* and *Janetaescincus*, on the Seychelles. The osteological similarities which align these skinks (11 premaxillary teeth, complete secondary palate involving both the palatines and pterygoids, large postorbital bone, and supratemporal fenestra) are striking and to me indicate close relationship instead of convergence. *Gongylomorphus* appears to be more primitive than *Pamelaescincus* and *Janetaescincus* in retaining a pair of frontoparietal scales, and *Pamelaescincus*, in turn, appears to be more primitive than *Janetaescincus* in lacking the posterior emarginations on the palatal rami of the pterygoids and in having 5 instead of 4 fingers.

Zoogeography

I now would like to make two very general comments about the zoogeography of the groups discussed above. First, if the size of the interparietal scale, i.e., whether it touches the supraocular scales or not, is truly indicative of relationship within the scincines of subsaharan Africa, Madagascar, and the west Indian Ocean islands, then we have two major groups with highly suggestive distributions. On the one hand, the scincines with the small interparietal are widely distributed throughout the area, whereas the scincines with the large interparietal are confined to continental Africa. Simply on the basis of the distribution of these two groups, it would be reasonable to argue that the more widespread group, i.e., the group that occurs on Africa, Madagas-

ear, and the islands of the west Indian Ocean, probably appeared in the area before the group that occurs only on the African mainland.

This interpretation has the support of the morphological data. The large interparietal of *Scelotes*, *Melanoseps*, *Scolecoseps*, and *Typhlacontias* is unusual in skinks and is probably derived from the small interparietal condition. The reduction and loss of the postorbital bone and the predominate trend toward burrowing habits in this group also imply its specialized evolutionary role. This evidence suggests that perhaps the large interparietal line evolved on continental Africa from the more widespread and less specialized small interparietal line.

The second zoogeographic point I wish to make concerns the Seychelles and Mauritius scincines. The single Mauritius genus (*Gongylomorphus*) and the two Seychelles genera (*Pamelaescincus* and *Janetaescincus*) appear to be each others closest relatives. There is a problem, however, in explaining how such closely related taxa can occur on two remote and widely separated oceanic island banks. The easiest explanation for this distribution might be that the three genera are simply relicts from a group of scincines that were once much more widely distributed over Africa and/or Madagascar. The flaw in this argument, however, is the notion that the complete secondary palate which unites the Mauritius and Seychelles scincines seems to be an extremely advanced character and is in no way primitive. That is, the complete secondary palate of these scincines appears to be an innovation unique to the scincines of the islands, and as the island banks were probably never connected in the past, skinks with this palatal character must have first appeared on one island bank and then dispersed over water to the second island bank.

The most likely method of over water dispersal for these skinks is by rafting. The probability of successful rafting is greatly increased by the availability of large rivers to carry detritus out to sea, but at present

neither the Seychelles nor Mauritius seems to offer a favorable source of rafts. In the recent, and perhaps more distant past, however, this was not the case. Whereas the volcanic Mauritius bank is relatively small (only slightly larger than the main island itself) and rises from very deep water, the largely granitic Seychelles lie on a very shallow, but relatively extensive (approximately 12,000 square miles), bank and would probably form "an extensive, low archipelago" with the standard Pleistocene lowering of sea levels. Under these circumstances large tropical rivers may have existed in the Seychelles and would perhaps have greatly increased the probability of dispersal from the Seychelles to Mauritius. If this were the direction of dispersal, we might visualize the primitive *Gongylomorphus* or its ancestor rafting from the Seychelles to Mauritius and surviving there as a relict while the parental stock became extinct on the Seychelles but was represented by the derived *Pamelaescincus* and *Janetaescincus*.

A KEY TO THE SCINCINE GENERA OF SUBSAHARAN AFRICA

Interparietal scale not touching supraocular scales; postorbital bone present and well developed.

Digital formula 5-5; pterygoid teeth lacking *Proscelotes*

Digital formula 4-4 or lower; pterygoid teeth present *Sepsina*

Interparietal scale touching supraocular scales; postorbital bone present but only weakly developed, or lacking entirely.

A single postrostral scale (fused supranasals); jugal bone lacking; 5-6 maxillary teeth *Typhlacontias*

A pair of postrostral scales (supranasals); jugal bone present; 10-23 maxillary teeth.

External naris well within an enlarged postrostral *Scolecoseps*

External naris near or bordering posterior edge of rostral scale.

Palatal ramus of pterygoid bone deeply emarginated posteriorly (Fig. 5) *Melanoseps*

Palatal ramus of pterygoid bone smoothly diverging along its postero-medial edge (Fig. 4) *Scelotes*

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SPECIMENS EXAMINED

I have seen the following complete skulls: *GONGYLOMORPHIUS*: *bojeri* MCZ 46677. *GRANDIDIERINA*: *lineata* MNHN 3378. *JANETAESCINCUS*: *braueri* BM 1910.3.18.33. *MELANOSEPS*: *ater* MCZ 50955, 52487; *occidentalis* BM 1907.5.22.6A. *PROSCÉLOTES*: *aenea* MCZ 18709; *arnoldi* MCZ 55145; *eggeli* MCZ 24217, 24218, 24220. *PAMELAESCINCUS*: *gardinieri* BM 1910.3.18.91. *PYGOMELLES*: *bracommeri* MNHN 1715. *SCÉLOTES*: *anguina* MCZ 96791; *arenicolor* MCZ 14205; *bidigitata* MCZ 96789; *bipes* BM XVII.2.F; *brevipes* MCZ 21237; *caffer* MCZ 96792; *gronovi* BM 97.5.15.8; *limpopoensis* MCZ 96906; *mira* MCZ 96790; *uluguruensis* MCZ 24206.

SCOLECOSEPS: *boulengeri* MCZ 18357. *SEPSINA*: *angolensis* FMNH 142793, AMNH 40734; *bayoni* BM RR 1967.80; *tetradactyla* MCZ 42885, 47770 (3 specimens), 47775, 56963, 56965, 56967, 85536. *TYPHILACONTIAS*: *brevipes* MCZ 96702; *gracilis* USNM 159338; *ngamiensis* FMNH 142787, 142791 (cleared and stained specimen). *VOELTZKOVIA*: *mira* MCZ untagged specimen. Malagasy *incertae sedis* "Scelotes": *astrolabi* MCZ 20953; *melanura* MCZ 11733; *splendidus* FMNH 72086.

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